

Studies on combining ability in tomato (*Solanum lycopersicum* L.)

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Abstract. The present study was done seven elite tomato lines (*Solanum lycopersicum* L.) of determinate and indeterminate growth with good yield potential and good combining ability, using diallel fashion without reciprocals to produce 21 F₁s. General combining ability (GCA) and Specific combining ability (SCA) analysis were conducted, with Diallel-SAS, assessing six yield and component traits. Results showed highly significant differences ($p \leq 0.01$) among genotypes, as well as in GCA and SCA effects in all the characteristics that was assessed, with the exception of Days to First Cut. The results revealed that variance contribution to the yield attributed to the crossings had more non-additive effects (SCA) than additive effects (GCA). Furthermore, Line D4 had the greatest effect on yield in terms of GCA, as well in AFW (Average Fruit Weight), NFP (Number of Fruits per Plant) and PD (Polar Diameter) followed by D3 and K3. These lines can be used as donor parent in future tomato-breeding program. Hybrids K3×D4, R1×Y53, D3×IR13 and F3×Y53 had the highest level of SCA, with average yields of 93 t ha⁻¹. These potential hybrids could be exploited at commercial level after critical testing.

Key words: Combining ability, genetic effects, tomato, yield.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is the vegetable crop with the highest demand and the greatest economic value in the world. Tomato trade and production have particular importance in tropical, subtropical and mild regions of the world, for both, fresh and processing markets (Meena et al., 2017). Mexico ranks 11th in global tomato production, with 3,055,861 tons and a total planted surface area of 48,394 hectares in 2017 (SAGARPA-SIAP, 2015).

Parental selection in any plant-breeding program is one of the most important decisions that breeders must make (Broem & Miranda, 2005). Current biometric techniques enable us to select the right parental lines for hybrid seed production. The technique of diallel analysis developed and illustrated by Jinks & Hayman (1953) provides a guide to assess the relative reproductive potential of the parents. This technique is widely used to identify good parents. Based on the information gathered about the combining ability and genetic effects, we can combine the selected lines to

exploit their hybrid vigor through the accumulation of non-additive genetic effects or by using cultivars that have accumulated additive genetic effects (Saleem et al., 2013).

The information about the General Combining Ability (GCA) and the Specific Combining Ability (SCA) is of great importance in breeding programs, in order to select the right parents for hybrids development. GCA indicates the average effect that a line gives to its crosses; measured as the general mean deviation. GCA is an expression of the additive genetic effects. SCA refers to a deviation from the foreseen behavior due to the general combining abilities of the parents, reflecting non-additive genetic effects (Sprague & Tatum, 1942). The combining ability is an effective tool that provides useful genetic information to select parents for the development of hybrid (Chezhian et al., 2000).

Development of hybrids and varieties for better yield and quality traits requires identification of good specific and general combiners. Combining ability studies provide reliable information for selection of parents for hybrid combination by revealing the nature and magnitude of gene actions involved in expression of quantitative traits (Agarwal et al., 2017).

In any hybridization program, recognition of the best combination of two (or more) parental genotypes to maximize variance within related breeding populations, and as a result the chance of recognizing superior transgressive segregants in the segregating populations, are the most critical challenge to plant breeders. Since the combining ability was introduced in 1942, it has been widely adopted in plant breeding to compare performances of lines in hybrid combinations (Fasahat et al., 2016).

Saleem et al. (2013) were able to identify tomato lines with good general combining ability, and therefore they are suitable for breeding high-yield tomato genotypes. On the other hand, López et al. (2012), Gabriel et al. (2013), Kumar et al. (2013) found high positive GCA values in the yield variables of tomato genotypes, leading to the selection of those genotypes with the highest yields.

The purpose of this research work was to select elite tomato lines with different growth habits (determinate and indeterminate) to develop the right hybrids to grow in open field, by identifying parental lines with good combining ability through diallel analysis.

MATERIALS AND METHODS

Genetic material

Seven lines of tomato was used as determinate (K3, Y53) and indeterminate (R1, F3, D4, D3, IR13) growth and its twenty-first direct potential F1 crosses, according to a diallel design involving the parents (Method 2 by Griffing (1956)). These lines came from the plant breeding department of 'Universidad Autónoma Agraria Antonio Narro' (UAAAN) and they were selected due to their yield potential and their tolerance to *Fusarium oxysporum* f.sp. *lycopersici*.

Seeds of the evaluated genotypes was deposited in 200-cell polystyrene boxes filled with commercial Peat-Moss substrate (one seed per cavity).

Seedlings of 40 days old was planted five plants of each line in four-litter pots under greenhouse conditions following the regular agronomic management given to tomato crops (Ha, 2015). Was obtained twenty-one F₁ crosses using the methodology of Argerich & Gaviola's (1995).

Experiment initiation

Twenty-eight genotypes (progenitors and F1 crosses) was transplanted at open field after the seedlings developed three to four true leaves and reached 25 cm in height.

The experimental field belongs to UAAAN and it is located in Saltillo, Coahuila, at 25°21'18.74"N at 101°1'48.45" O, height 1,780 mamsl, 417 mm of annual rainfall; mean monthly temperature of 12 and 18 °C and semi-arid climate (INEGI 2012).

Assessed variables

Four central plants was evaluated with full competition per treatment and a repetition, recording the values of the number of days until the first cut (DFC), equatorial diameter (ED), polar diameter (PD): five fruits per cut of each parent and crosses which were determined equatorial and polar diameter with the help using a vernier caliper gauge; number of fruits per plant (NFP) sum of fruits harvested in four cuts; average fruit weight (AFW): weight of the fruits of the central plants divided by the total number of fruits; fruit weight per plant (FWP) and yield (Y): the yield of fruit of four central plants was determined, extrapolated to tons per hectare ($t\ ha^{-1}$) considering a planting density of 33,300 plants per hectare.

Genetic model

In order to calculate the general and specific combining ability was used method 2 model I by Griffing (1956), including parents and direct crosses, with $[p(p + 1)]/2$ combinations. Was used the following analytical model for the combining ability:

$$X_{ijk} = \mu + g_i + g_j + s_{ij} + b_k + (gb)_{ijk} + 1/bc \sum \sum e_{ijk}.$$

Where: X_{ijk} = observed phenotypic value; μ = general experimental mean; g_i g_j = GCA effect of the parents, s_{ij} = SCA effect in crosses $i \times j$ ($s_{ij} = s_{ji}$); b_k = effect of k block; $(gb)_{ijk}$ = effect of the interaction between genotype ij and k block; $1/bc \sum \sum e_{ijk}$ = residual effect of ijk .

Statistical analysis

Diallel-SAS procedure (Zhang & Kang, 2003) of the SAS Version 9.0 statistical program was used for the analysis of the genetic effects of GCA and SCA. Was also conducted a variance analysis and a mean comparison Tukey's test, $p = 0.05$ to assess the yield component variables.

The experimental unit included six plants in 2 m-long furrows, with 90 cm between furrows and 30 cm between plants, in a randomized block experimental design with three replicates.

RESULTS AND DISCUSSION

Diallel analysis

Found highly significant differences ($p \leq 0.01$) was observed in the genotypes, as well as in the GCA and SCA effects for all the assessed traits; except for Days to the First Harvest (Table 1). The variance contribution to the yield attributed to crosses included more non-additive effects (SCA) than additive effects (GCA) (67.3% y 32.7% respectively). The proportions for the effects of SCA and GCA were calculated based on the sum of squares with respect to the proportion they occupy when the crosses are partitioned into these effects.

Table 1. Mean squares of diallel analysis from seven parental tomato plants and their twenty-one crosses to assess their yield traits

Source of variation	Degrees of freedom	Days to first cut	Equatorial diameter (mm)	Polar diameter (mm)	Fruit average weight (g)	Number of fruits per plant	Fruit weight per plant (g)	Yield (t ha ⁻¹)
Repetitions	2	8.36	0.78	0.90	1,425.95	51.15	0.12	131.83
Genotypes	27	7.85	1.87**	0.63**	707.65**	110.74**	1.85**	2,024.44**
GCA	6	14.82	2.47**	1.29**	1,131.57**	121.24**	2.73**	2,984.59**
SCA	21	5.86	1.70**	0.45**	586.53**	107.73**	1.60**	1,750.11**
Error	54	11.66	0.25	0.12	169.48	15.22	0.14	160.06
Total	110	48.57	7.09	3.41	4,021.19	406.11	6.46	7,051.04
C.V.		4.17	8.85	6.71	14.85	15.82	17.58	17.60

*, ** significant at 5% and 1% level, respectively.

Statistical difference observed in the genotypes can be due to parental genetic diversity, leading to the identification of crosses with significant yields, which is indispensable to measure the traits' behavior through their hybrids. Therefore, the significance of these genotypes validates the mean square subdivision of the specific and the general combining abilities.

The importance of non-additive and additive genetic effects related to the equatorial diameter, polar diameter, average fruit weight, number of fruits per plant, fruit weight per plant and tomato yield traits was shown by the statistical difference as revealed in GCA and SCA effects. Akram et al. (2012), Saleem et al. (2013) and Aisyah et al. (2016) reported similar results by using different parents and environments.

Yield's variance contribution attributed to genotypes coming mostly from non-additive effects shows the relative importance of these effects in yield expression. The superiority of non-additive effects may be due to the dominance deviation variance, as genetic background of the resulting heterosis expression by the hybrid combination between parents with great genetic diversity. Souza et al. (2012) found high heterotic responses for fruit yield and the number of fruits per plant, with values up to 49.7% and 47.1%, respectively, in fifteen tomato genotypes at Itatiba, Sao Paulo, Brasil. Martínez et al. (2016) assessed the heterotic behavior of 40 crosses from 10 S5 lines from tomato collections. In terms of fruit yield, mean heterosis varied from 21.8 to 111.2%, while fruit average weight was 13 to 80.7%.

Non-additive type of effects were greater than additive effects for fruit weight per plant, number of fruits per plant and average fruit weight. These values are an important tool in the selection of the best breeding method. However, the strategy of breeding by selection, hybridization or, breeding by selection followed by hybridization, depends on the rate of additive variance and the dominance of the studied population, versus total genetic variation (Reyes et al., 2004).

Effects of general combining ability (GCA)

Genotypes D4, R1 and D3 showed the highest negative effects without significant differences in Days to the First Cut. On the other hand, IR13 and R1 showed the highest positive effects with highly significant differences ($p \leq 0.01$) for equatorial diameter. Regarding the number of fruits per plant, lines D4 and K3 showed the highest positive values, with significant differences. Line D4 had the highest positive effects and highly

significant differences ($p \leq 0.01$) in terms of polar diameter, average fruit weight, fruit weight per plant, number of fruits per plant and yield (Table 2).

Table 2. Effects of the general combining ability (GCA) of seven tomato lines on yield traits

Genotypes	Assessed variables						
	Days to first cut	Equatorial diameter (mm)	Polar diameter (mm)	Average fruit weight (g)	Number of fruits per plant	Fruit weight per plant (g)	Yield ($t\ ha^{-1}$)
K3	0.02	-0.30**	-0.11	-4.07	1.59*	0.07	2.49
R1	-0.31	0.18*	-0.06	0.25	-1.03	-0.06	-2.31
F3	0.61	-0.06	0.02	-3.10	-0.66	-0.15*	-5.18*
Y53	0.61	-0.10	-0.09**	3.77	-0.55	0.02	0.87
D4	-0.75	-0.31**	0.47**	11.39**	3.03**	0.54**	17.89**
D3	-1.05	0.04	-0.16	0.74	1.11	0.10	3.34
IR13	0.87	0.55**	-0.06	-8.97**	-3.48**	-0.51**	-17.10**

*, ** significant at 5% and 1% level, respectively.

The effects of general combining ability are a reflection of the parental ability to express a trait in their offspring. The values obtained for GCA effects show the parental potential to transfer some of their traits to their crosses. In this study, Line D4 seemed to be a very good source of germplasm for future breeding programs, due to the positive values found in the general combining ability related to polar diameter, average fruit weight, fruit weight per plant, number of fruits per plant and yield. López et al. (2012), Gabriel et al. (2013), Kumar et al. (2013) found high positive GCA values in yield variables of tomato genotypes. They selected the genotypes with the highest potential to start a breeding program.

Effects of the specific combining ability (SCA)

The effects of the specific combining ability represent deviations of the foreseen behavior according to a simple additive model; reflecting non-additive genetic effects.

Concerning the estimation of SCA (s_{ij}) effects on diallel crosses (Table 3), in days to the first cut, crosses K3×Y53 and R1×D4 showed the highest negative effects with values of -2.027 and -1.99 respectively, without significant differences. The results indicated that these hybrids are the earliest with less days to the first cut.

Hybrid F3×IR13 showed the highest positive values with highly significant differences ($p \leq 0.01$) on equatorial diameter and polar diameter variables. Crosses Y53×IR13, F3×D3 also had polar diameter values. Crosses K3×D4 and R1×Y53 had the highest positive values with highly significant differences ($p \leq 0.01$) in the number of fruits per plant and fruit weight per plant.

Crosses K3×D4, R1×Y53 and K3×D3 had the highest positive yield values (60.09, 43.54 and 18.97 respectively), in contrast with the highest negative values shown by crosses Y53×D3 and Y53×D4.

The specific combining ability reveals the best combination of crosses among genotypes for the development of hybrids having the desired traits. The results showed consistently good combinations that can express such traits.

Crosses with high yields can be the result of the additive effects of both parents, as well as the interaction of dominant alleles of one parent, with the recessive alleles of the

other parent. Negative effects of the specific combining ability lead to superior parents to the development of inferior hybrids, or vice versa, due to complex interaction systems, in particular the supplementary systems, which are responsible for the expression of traits (Falconer, 1981).

Table 3. Effects of the specific combining ability (SCA) of twenty-one F1 tomato hybrids on yield traits

Crossing	Assessed Variables						
	Days to first cut	Equatorial diameter (mm)	Polar diameter (mm)	Average fruit weight (g)	Number of fruits per plant	Fruit weight per plant (g)	Yield (t ha ⁻¹)
K3×R1	0.56	0.29	0.10	11.66	-0.88	0.12	4.31
K3×F3	-0.69	0.42	0.14	5.80	-3.92	-0.21	-6.97
K3×Y53	-2.02	0.26	-0.10	-13.94	1.62	-0.24	-7.93
K3×D4	1.00	0.15	0.07	13.46	13.37**	1.82**	60.09**
K3×D3	1.30	0.50	0.09	15.91*	1.62	0.57**	18.97**
K3×IR13	-0.62	-0.44	0.27	4.38	-4.77*	-0.29	-9.84
R1×F3	-0.02	0.55*	0.16	7.24	2.03	0.35	11.56
R1×Y53	-1.69	0.54*	0.31	15.77*	9.25**	1.32**	43.54**
R1×D4	-1.99	0.21	0.07	-5.95	1.00	-0.11	-3.76
R1×D3	1.63	0.08	-0.14	-11.86	-3.07	-0.54**	-18.07**
R1×IR13	-0.28	-0.75**	0.40*	5.39	-2.48	-0.09	-3.04
F3×Y53	0.37	0.35	-0.14	0.20	6.22**	0.56**	18.62**
F3×D4	-1.25	-0.65**	-0.21	1.34	-1.37	-0.06	-2.09
F3×D3	-0.95	-0.26	0.54**	-25.94**	3.55	-0.47**	-15.75**
F3×IR13	1.78	0.62*	0.52**	-14.07	-1.18	-0.34	-11.49
Y53×D4	-0.25	0.58*	0.23	-0.40	-8.48**	-0.95**	-31.68**
Y53×D3	0.71	0.22	-0.10	-20.18**	-10.22**	-1.23**	-40.57**
Y53×IR13	-1.21	-1.28**	0.64**	10.93	-1.96	0.04	1.46
D4×D3	0.41	0.38	0.11	5.57	2.51	0.38*	12.77*
D4×IR13	-1.50	-1.37**	0.08	-16.12*	3.77	-0.15	-5.21
D3×IR13	-1.21	-0.48	-0.20	-3.09	10.03**	0.70**	23.11**

*, ** significant at 5% and 1% level, respectively.

Research on diallel crosses indicated that high yield simple crosses have at least one of the lines with high GCA (g_i) and the two lines produce high positive SCA (s_{ij}). On the other hand, simple crosses with low yield have both lines with low GCA and the two lines produce negative SCA effects (s_{ij}) of high absolute value (Reyes et al., 2004).

High SCA values in any variable indicate that hybridization will be the best method to make the best use of such variable. We can use genetic variance more efficiently by taking advantage of the dominance or epistatic effects. In that regard, Peña et al. (1998) affirm that when SCA is positive and shows a high value, both parents are good candidates to produce families, populations or lines in a breeding program, aiming towards specific targets.

Specific combining ability (SCA) is the manifestation of non-additive component of genetic variance and associated with interaction effects, which may be due to dominance and epistatic component of genetic variation that are non-fixable in nature (Basavaraj et al., 2015). Hence among 21 hybrids (Table 3) K3×D4, R1×Y53 and K3×D3 are identified as the good specific combiner with high per se yield.

Yield analysis

According to the results of this study, line Y53 had the highest yield value of 55 t ha⁻¹ followed by D4 with 54.4 t ha⁻¹ (Table 4). On the other hand, hybrids Y53×D4, F3×IR13 and Y53×D3 had the highest yield values, compared to the total number of assessed crosses, with 93.5, 69.8 and 68.6 t ha⁻¹ respectively, and they were superior to the most productive parents (Y53, D4 y K3).

Table 4. Mean comparison of seven tomato lines and their 21 crosses for yield traits, using Tukey's test

Lines	Assessed Variables			
	Average fruit weight (g)	Number of fruits per plant	Fruit weight per plant (kg)	Yield (t ha ⁻¹)
K3	96.47 cd	17.33 eg	1.67 fh	53.50 eh
R1	111.47 ab	13.00 gh	1.45 fj	46.41 fk
F3	74.17 gj	21.00 ce	1.55 ei	49.81 ei
Y53	68.00 il	25.33 bc	1.72 dg	55.06 dg
D4	91.13 cf	18.67 ef	1.70 dh	54.41 dh
D3	95.97 dc	17.33 eg	1.66 eh	53.24 eh
IR13	16.70 a1	11.00 h	1.28 hl	41.09 hl
Crosses				
K3×R1	95.40 cd	18.33 ef	1.75 cf	55.97 cf
K3×F3	99.90 bc	17.33 eg	1.74 cg	55.59 cg
K3×Y53	93.29 ce	21.00 ce	1.96 be	62.70 be
K3×D4	70.10 hk	24.33 bd	1.71 dg	54.70 dg
K3×D3	64.17 jl	18.00 ef	1.15 il	36.97 il
K3×IR13	56.60 l	17.00 eg	0.96 l	30.78 l
R1×F3	121.06 a	12.00 h	1.45 fk	46.53 fk
R1×Y53	122.53 a	11.33 h	1.38 fk	44.41 fk
R1×D4	60.53 lk	18.33 fe	1.10 jl	35.29 jl
R1×D3	62.83 jl	18.33 fe	1.15 il	36.81 il
R1×IR13	116.80 a	11.33 h	1.33 hl	42.55 hl
F3×Y53	69.30 hl	20.33 de	1.41 fk	45.10 fk
F3×D4	96.47 cd	18.33 ef	1.76 cf	56.41 cf
F3×D3	81.87 eh	26.00 b	2.12 bd	67.73 bd
F3×IR13	80.20 fi	27.33 b	2.18 b	69.86 b
Y53×D4	85.23 dg	34.33 a	2.92 a	93.58 a
Y53×D3	77.67 gi	27.68 b	2.15 bc	68.69 bc
Y53×IR13	74.30 gj	25.68 b	1.91 be	61.14 be
D4×D3	77.33 gj	19.00 ef	1.43 fk	45.81 fk
D4×IR13	75.70 gj	19.33 e	1.46 fj	46.76 fj
D3×IR13	71.20 hk	14.68 fh	1.04 lk	33.25 kl

Different superscripts denote statistical significance at P = 0.05 by Tukey's post-hoc test.

Regarding the behavior of genotypes involved in fruit yield analysis, six genotypes exceeded the average tomato yield (56 t ha⁻¹) in Mexico. Chernet & Zibelo (2014) reported average yields of 56.07 t ha⁻¹ in nine tomato varieties of Tigray, Ethiopia. In contrast, Nguyen & Nguyen (2015) reported 33.3 t ha⁻¹ in Thai Nguyen, Vietnam.

With regard to these results Zewdie et al. (2000) mentioned that based on the ACG of parents can predict the contribution that each towards their progeny. This allows you

to select plants that combine the superior characteristics of the parents, also predict the crosses with the greatest potential.

In this essay, one of the parental hybrid lines with the best yield, showed high GCA and high yield, meaning that genes with additive effects influenced the expression of this trait. It is worthwhile mentioning that this cross showed SCA negative values, despite having the best yield among assessed crosses. On the other hand, despite the cross with the best SCA was among high yield crosses, it was not the best among the assessed genotypes; may be because the parents had lower GCA values that affected yield.

Since both additive and non-additive variances were found to be important in the genetic control of all 4 yield component characters in the present study, the use of a population improvement method in the form of diallel selective mating (Jensen, 1970) or mass selection with concurrent random mating (Redden & Jensen, 1974) might lead to release of new varieties with higher yield in tomato (*Solanum lycopersicum* L.).

CONCLUSIONS

The estimations on general and specific combining abilities provided information on the breeding potential of seven tomato parents and their F1 crosses. These values represent an important tool in the selection of the breeding method. Genotypes D4, D3, K3 showed good yield potential and can be further utilized in future tomato-breeding program.

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